A STUDY OF THE CARYODIDAE (PULMONATA) PART II: *CARYODES DUFRESNII* (LEACH 1815).

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ABSTRACT

A neotype for the Tasmanian terrestrial snail *Caryodes dufresnii* (Leach 1815) is erected and described. The anatomy of *Hedleyella maconelli* (Reeve 1853) from Queensland is described and comparisons made between these species and other Tasmanian caryodid morphs. The genus *Caryodes* Albers 1853 is diagnosed.

INTRODUCTION

A search for type material of the Tasmanian endemic land snail *Caryodes dufresnii* (Leach 1815) has not been successful. Three subspecies introduced by Iredale (1937) are known only by the figures designated by Iredale. The anatomy of possible representatives of these "subspecies" has been studied and will be described in the next part of this series (Kershaw unpublished). During the course of anatomical studies for the present work several other variably distinct morphs were noted. For these reasons it has been necessary to determine the type locality accurately and to attempt to locate type material.

The search for type material has been discussed and the proposed type locality defined elsewhere (Kershaw 1987). The purpose of this paper is to erect a neotype, describe the anatomy and to compare this with other known morphs. Further detailed animal and shell variation studies will be required to determine the taxonomic status of these morphs.

Despite the loss of many populations since European settlement this snail is still widespread within Tasmania excluding the Bass Strait islands. It has been generally assumed that only one variable species is present although small distinct shells have long been known. These came from woodland localities long cleared for rural purposes but in recent years live specimens have been found. The addition of live large morphs from the more remote wet forests has made a study of the anatomy possible.

PREVIOUS LITERATURE

The first paper of this series deals with the anatomy of the species *Anoglypta launcestonensis* (Reeve 1853) (Kershaw 1988). The anatomy of *Caryodes dufresnii* has been studied by Semper (1874), Hedley (1892), Pilsbry (1894) and Davies (1914). Davies dissected an animal from Port Esperance which appears to be one of the small morphs. She added detail on the kidney, heart and alimentary system to the earlier knowledge. Although two Mt. Wellington specimens are mentioned these may not have been dissected. Chromosome numbers were established by Dartnall and Dartnall (1972) who provided some comments on the genitalia and taxonomy.

A long discussion by Tenison-Woods (1878) deals with the early knowledge of the species and refers to the shell variation as understood. Kershaw & Dartnall (1972, 1975) provide further historical and variation data. Descriptions of the shell were provided by Cox (1868), Legrand (1871) and Petterd (1889). Additional detail on relationships was provided by Germain (1925) and Solem (1969, 1979).

An attempted revision of the classification by Iredale (1937) has not been accepted by Zilch (1960) nor subsequent authors including Smith & Kershaw (1981). The present work proposes no change to the classification of Solem (1978).

MATERIAL AND METHODS

The proposed neotype together with four associated specimens here designated as vouchers are held in the Tasmanian Museum and Art Gallery collection. All the specimens of the genus *Caryodes* in that Museum and the Queen Victoria Museum and Art Gallery have been studied. The author's collection of more than 50 lots containing most of the dissected material will be lodged in the Queen Vistoria Museum and Art Gallery collection. The 26 specimens dissected for this paper were selected from 19 localities (Table 1). The specimen of *Hedleyella maconelli* described was provided by Charles Horton from 10 miles east of Gympie, Queensland. Scanning electron micrographs of the *Caryodes dufresnii* radula made by Adrian Daniell of La Trobe University were compared with micrographs by Dr. B. J. Smith.

All dissections, drawings and measurements were made using a Zeiss dissecting microscope with drawing attachment. Shell measurements were made by use of a vernier scale. Grid references provided refer to the 1:100 000 Topographic Survey of Tasmania published by Tasmap.

Genus *Caryodes* Albers 1850
Haplotype *Bulimus dufresnii* Leach 1815.

DIAGNOSIS

Shell: (fig. 1) An elongate ovoid shell with a variably narrowly obtuse spire, convex whorls usually distinctly banded, not keeled, rarely umbilicate, which has a variably coloured dull epidermis. The sculpture, originating on the protoconch is strongly spirally reticulate fading variably to punctate or so that only weak radial ridges are clearly visible. The aperture although changing with growth, is vertically or obliquely more or less pyriform with thickened outer margins and a reflected columella in the adult.

Animal: (fig. 2) A variably coloured snail of the Caryodidaie with unicuspid teeth mounted on short broadly rounded basal plates. The penis is elongate with a narrowly produced more or less hooked apical region into which the male pore opens. The vas deferens enters the penial wall approximately adjacent the retractor at about two thirds the penis length. The epiphallic region is marked by a slight increase in the diameter of the duct over the region attached to the penis and a change in internal structure from simple pilasters to beaded pilasters. The male pore is a transverse or longitudinal orifice lined with short pilasters which merge with epiphallic structure. The very short free oviduct is lined with a variable pattern of fine laminate ridges. The bursa duct diverticulum, internally of distinct structure, variable in length and coiling has its apex directed away from the atrium.

The carrefour region consists of a moderately distinct talon and elongate duct receiving the albumen gland duct, entering an apparent almost "S" shaped perivitelline membrane gland (Tompa 1984). The vagina structure may include a large pad-like pilaster and/or a variably deep pocket or neither of these. The ovotestis consists of 7 lobes of elongate folicles embedded in the digestive gland surface.

DISCUSSION

A description of *Caryodes* was given by Pilsbry (1894) who noted the primary ureter opening at the kidney base. Both Pilsbry and Tenison-Woods (1878) describe the large eggs. Further discussion on the eggs with a description of juveniles was given by Kershaw & Dartnall (1972, 1975).

The sperm duct does not enter the penis terminally as illustrated by Dartnall & Dartnall (1972). The tendency for the narrowed extremity of the penis to become hooked (fig.13) or coiled due to the action of the retractor was probably responsible for their observation.

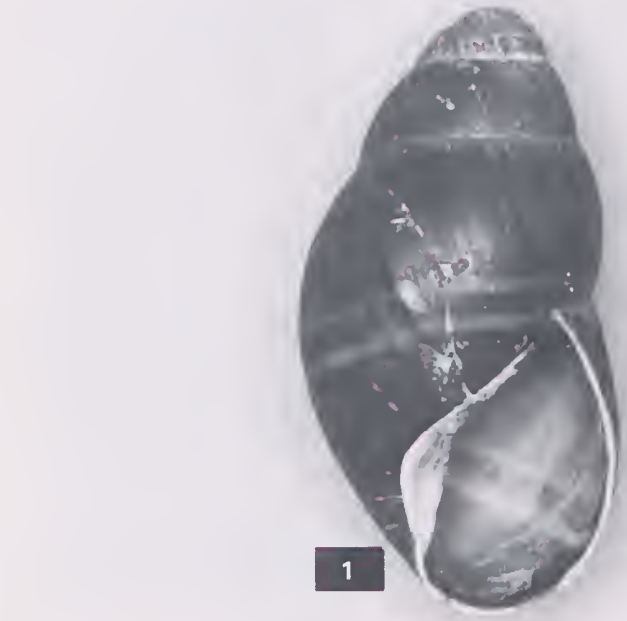


Figure 1. *Caryodes dufresnii* (Leach) Shell, South Cape Bay, Height 36 mm.
Figure 2. *Caryodes:* the animal; length crawling 50 mm.
Figure 3. *Caryodes dufresnii:* neotype; height 36.2 mm.

Remarks on the resemblances in the protoconch sculpture between *Caryodes* and *Anoglypta* are presented in part I of this work (Kershaw 1988). *Anoglypta* differs noticeably in the simpler structure of the carrefour-membrane gland region. *Anoglypta* has half the number of teeth per row, a much simpler pallial venation pattern and the diverticulum is short and reversed. The penial structure of elongate laminar pilasters is similar in both animals which clearly are ancestrally closely related.

Caryodes is a complex of morphs apparently adapted to different ecological niches throughout its range, each morph having evident distinction approaching the species level. *Anoglypta* is a highly specialised snail with several racial morphs all apparently adapted to the same basic ecology within a limited range. Although sympatric within the *Anoglypta* range these snails show little evidence of interspecies competition on present knowledge.

Caryodes dufresnii (Leach 1815).

Neotype (fig. 3): Tasmanian Museum Registered number E 16803; one shell of five whorls of dimensions 36.2 mm height, 19.3 mm maximum diameter, aperture 18.3 mm height, 10 mm width, collected by Miss Jane Burrell in leaf litter in wet forest near South Cape Bay, South Tasmania between 30 June and 1 July 1973, complete with animal preserved in alcohol.

Vouchers: Three specimens Tasmanian Museum Registered Number E 8591a of dimensions:
5.5 whorls, ht. 36.9, diam. 20, aperture 19.2 by 10.4 mm.
5.0 whorls, ht. 36.4, diam. 19, aperture 19 mm ht.
5.0 whorls, ht. 31, diam. 18, aperture 17.2 by 9 mm.

One specimen dissected with genitalia preserved separately Registered Numbers E8591b and E8591c of dimensions:
5.2 whorls, ht. 36, diam. 19.1, aperture 19 by 9.4 mm. all specimens from the one locality.

Type Locality: "Australasia" Leach (1815) redefined as the region between Recherche Bay and South Cape Bay bounded by 43°31′S to 43°37′S and 146°44′E to 146°53′E (Kershaw 1987).

DIAGNOSIS

A large elongate bulimoid imperforate shell having a variably obtuse apex, of 5 or more whorls in the adult in which the reflected columella is twisted so that the base is more or less broadened. The animal has a penial structure of longitudinal pilasters with fluted sides and oblique pilasters, a large male pore at a distance from the penial apex, a long bursa duct diverticulum, a vagina pocket together with more or less complex internal structure in the vagina and diverticulum.

Description

The Shell: The greenish brown yellow spotted convex protoconch (fig. 4) has at least 2.5 whorls sculptured with bold slightly spaced spiral ribs with weaker spiral riblets between, increasing to about 25 on the second whorl and radial ridges which produce irregular raised nodules strongest at the suture. The protoconch ends between 2.5 and 2.75 whorls with closer narrower radial ridges but the basic pattern continues into the adult.

The Adult sculpture (figs. 1, 5) consists of irregular radial ridges raised below the suture and close spiral lirae cut into a decussate pattern of squared and elongate pustules in regular lines which weaken with growth.
The Neotype (fig. 3) at 5 whorls is subadult with a slightly obliquo pyriform aperture having the outer margin moderately thickened, the columella slightly twisted and the base broadly rounded. The colour is red brown to dark brown with the paler spire tinted yellow brown to greenish with weak yellowish streaks. There are two narrow yellow and one wide dark brown bands above the dark reddish brown base.

The Animal: The dissected specimen, having a shell of 5.2 whorls and an almost adult aperture (fig. 1) is a strong well grown animal with a well developed muscular system. The

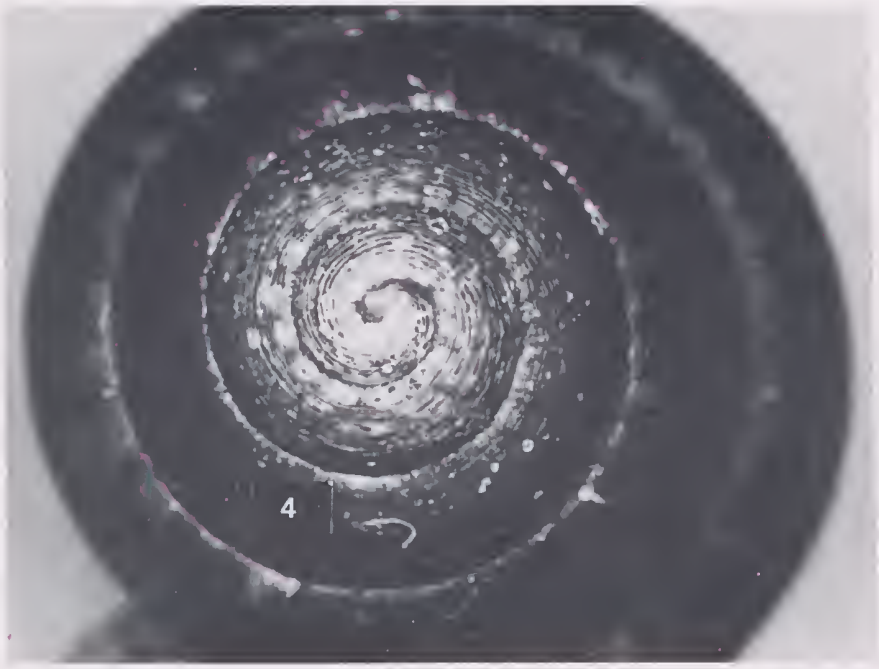


Figure 4. *Caryodes dufresnii:* protoconch.
Figure 5. *Caryodes dufresnii:* sculpture of the spire.

foot and body colour is pale brown or pinkish cream with the sole pinkish pale cream. The foot ornament consists of flattened subangular to rounded tubercles with close clear marginal lobes passing as depressed lines on to the sole, becoming larger posteriorly.

The Jaw is shallowly arcuate, orange to yellowish dorsally with sculpture of faint longitudinal and transverse lirae, weak ridges and no median projection.

The Radula (fig. 29) consists of numerous rows of unicuspid moderately broad elongate teeth set on strong columns arising anteriorly from short broadly rounded basal plates. There are 101 teeth per row with an approximate formula of 38.12.1.12.38 (Semper (1874) counted 81 to 87). There are two transitional areas. Teeth numbers 10 to 12 are transitional from laterals to latero-marginals and teeth 22 to 27 are transitional to the marginals.

The Central tooth (fig. 30) is elongate wedge shaped, slightly raised anteriorly, distinctly impressed with an antero-central longitudinal line more deeply impressed at 3 points. The pointed cusp is distinctly shorter than adjoining laterals and commonly worn. The basal plate (fig. 31) has 2 raised lateral flanges somewhat compressed posteriorly and a slim column supporting the cusp. Northern and eastern morphs studied have a raised anterior swelling, no central depression and a broader basal plate. In all cases the anterior margin engages smoothly between the flanges of the next tooth in line.

The Lateral Teeth (fig. 30) are kite shaped, broader more elongate than the central tooth (fig. 30) with a clearly raised anterior flange. The support column is distinctly expanded toward the central tooth with each tooth recessing in the column of its neighbour. The basal plate (fig. 31) has a distinctly raised flange on the outer margin. The anterior flange is more produced in transitional tooth no. 10 and increasingly narrowed in teeth 11 and 12.

The Latero-marginal Teeth are slightly longer with the anterior flange narrowed and the teeth have an oblique orientation. In the transitional region between nos. 22 to 27 the teeth become shorter and more rounded.

The Marginal Teeth (fig. 32) are narrow elongate digitiform with little or no anterior flange.

Cusp Wear (figs. 30, 33). The cusps are commonly rounded and fracture appears frequent. Grooves are cut longitudinally in the central and lateral teeth and obliquely across the latero-marginals and marginals reflecting the orientation during feeding. Daniell when photographing the teeth suggested a chisel-like action for the central and first lateral teeth while the oblique marginals may have a knife action. Cusps are serrated due to the numerous chips. The Interlocking interaction (figs. 30, 31) between each tooth and plate with anterior, posterior and lateral neighbours is similar to that observed in *Anoglypta launcestonensis*. At the start of the feeding action the cusp anterior margin is interlocked with the basal plate of the next tooth in line.

ANATOMY

The Foot Cavity (fig. 6) is short and contains the terminal genitalia, the elongate buccal mass, anterior oesophagus, pale cream salivary gland, the circumoesophageal ganglionic ring and the anterior muscalature.

The digestive system (fig. 7) is elongate with the stomach marked with pale lines, the intestine coils within the pale brown digestive gland above the stomach. The rectum has short pilasters near the anus as found in *Anoglypta*.

The Pallial region (fig. 8) is very elongate with a very strongly developed circulatory system. The large heart (fig. 8) laterally adjacent the kidney has no immediate branching of the aorta.

The Kidney (fig. 9) is elongate almost cylindrical subtriangular with the distinct primary ureter opening at the base into the pallial cavity adjacent the rectum. Solem (1976b) compares this to the Endodontidae structure.

REPRODUCTIVE ANATOMY

Apical Genitalia (fig. 10). The ovotestis consists of 7 globular lobes of elongate follicles. The hermaphrodite duct is very long and strongly kinked with seminal vesicles when mature

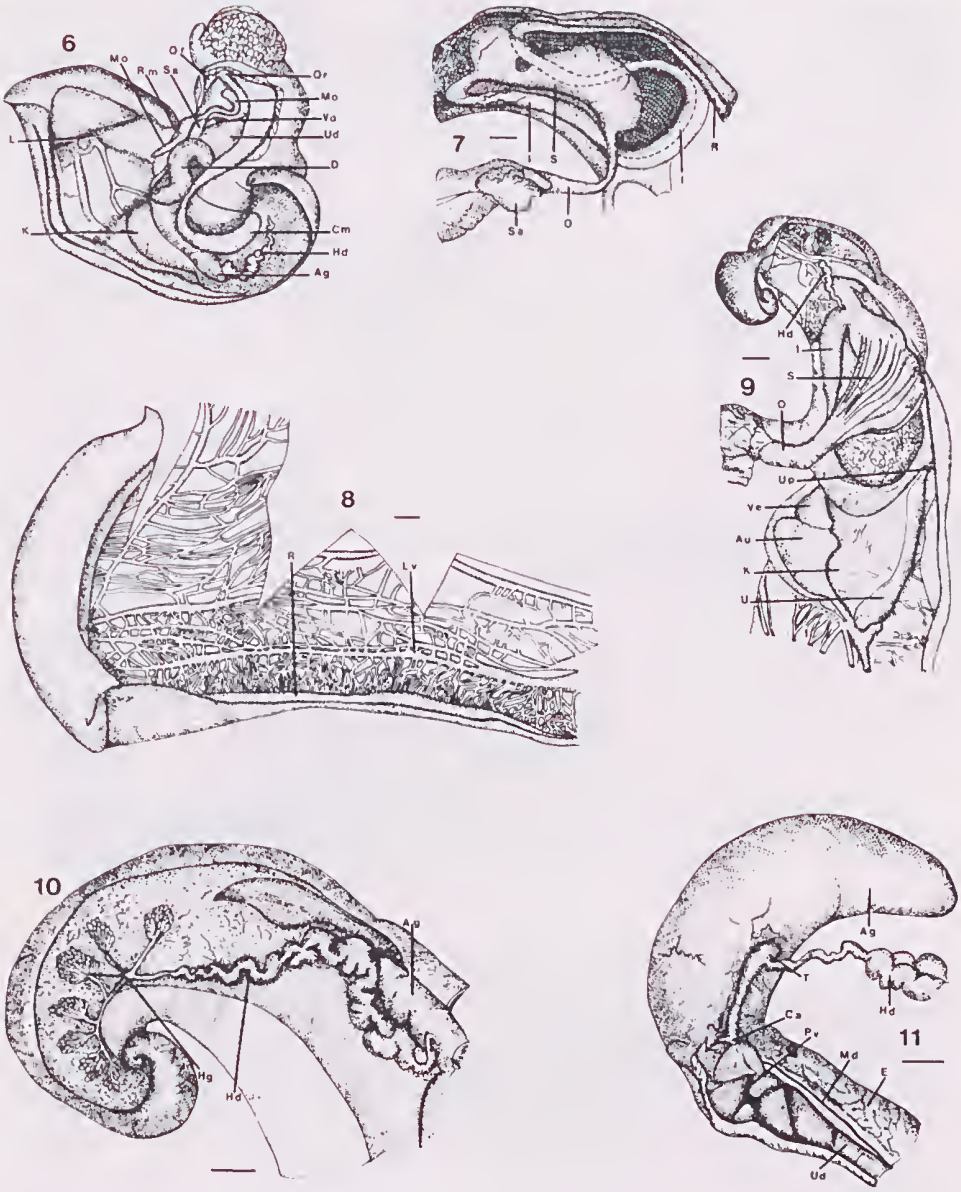


Figure 6. *Caryodes:* Kingston animal with pallial surface lifted and foot anatomy exposed, scale 2 mm.
Figure 7. *Caryodes:* Mt. Wellington animal digestive system, scale 2 mm.
Figure 8. *Caryodes dufresnii:* pallial venation, scale 2 mm.
Figure 9. *Caryodes dufresnii:* the kidney (K), ureter (U) and heart, scale 2 mm.
Figure 10. *Caryodes:* Port Davey animal, ovotestis (Hg), scale 2 mm.
Figure 11. *Caryodes:* Maria Island animal, carrefour region (Ca) and proximal common duct, scale 2 mm.

(an example measured 34 mm) entering the elongate hooked talon latero-apically. The carrefour region including the 2 mm talon (fig. 11) is largely embedded in the albumen gland with the albumen gland duct joining the complex just prior to entry to the somewhat "S" shaped perivitelline membrane gland (fig. 11). The common duct then opens to a capacious uterus and very narrow semi-enclosed male duct.

The Albumen Gland (fig. 12) small digitiform and cream coloured when immature thickens and colours orange with maturity.

THE SPERMOVIDUCT

The Common Duct (fig. 12) is elongate narrow with a thin greyish white immature uterus which expands and colours light cream with maturity. The prostate expands similarly passing through pinkish cream to deep cream in the male phase.

The Bursa Copulatrix (fig.12) is a small globular body immersed in digestive gland tissue adjacent the kidney base and the intestine as in *Anoglypta*.

The Bursa Duct (fig. 13) is an elongate fine tube attached for most of its length to the common duct entering the vagina apically opposite the free oviduct but expanding to a junction region. Internally the bursa duct is lined with low broad transversely marked pilasters.

The Bursa Duct Diverticulum (fig. 12, 14) is of medium length narrow elongate entering the bursa duct through a narrow pore just short of the vagina junction. The internal structure consists of narrow fleshy rather irregular pilasters which are irregularly transversely lined and joined apically with low narrow transverse ridges. The diverticulum is bound tightly to the common duct surface with its apex directed away from the atrium.

The Vagina (fig. 12, 14) is a short compact but capacious chamber which receives the free oviduct apically and has a small bulging pocket basally adjacent the atrium. The chamber is lined with broad low pilasters which become more diverse then narrower near the atrium in the pocket region. The oviduct is free briefly following bifurcation from the vas deferens and lined with fine pilasters to its pore in the vagina wall. The bursa duct-vagina junction is short and variably structurally distinct although functionally it is part of the vagina.

The Atrium is very short, 4 mm or less, opening through a relatively inconspicuous gonopore near the right ocular tentacle. Thus both male and female pores are close to the exterior but the vagina orientation is lateral to the penis. The male pilasters are broad and the female, narrow.

MALE GENITALIA

The right ocular tentacle retractor passes over the penis and between the oesophagus and spermoviduct (fig. 6). The Vas Deferens (figs. 12, 15) is a short narrow duct which emerges almost immediately from the prostate to coil about the vagina to the penis. The epiphallic portion is tightly appressed to the penial wall to enter at 50% of the length. There is a consequent external and internal bulge to the male pore at about 6.5 mm from the apical extremity. The pore is a curved slit surrounded by a rather fleshy wall projecting into the lumen. The bulging adjacent region is marked with small irregular slits. Internally the vas deferens is lined with oblique closely beaded narrow pilasters. These develop from simple thin pilasters at about half the length to become more complex near the pore where there are short longitudinal pilasters (fig. 15).

After coiling about the vagina the vas deferens is very narrow until it reaches the penis where there is a small but distinct expansion over the epiphallic region. Although there is a change in the internal structure no spermatophore has been recognised and hence the functional significance is uncertain. It is barely comparable to the distinctly swollen epiphallic region of *Hedleyella maconelli*.

The Penis (fig. 12, 16) is elongate (26 mm) thin medially inflated subcylindrical tapering to acuminate apically. Internally the structure is of 12 close rounded pilasters in the narrow basal region and about 25 medially. Adjacent the region of vas deferens emmersion and on

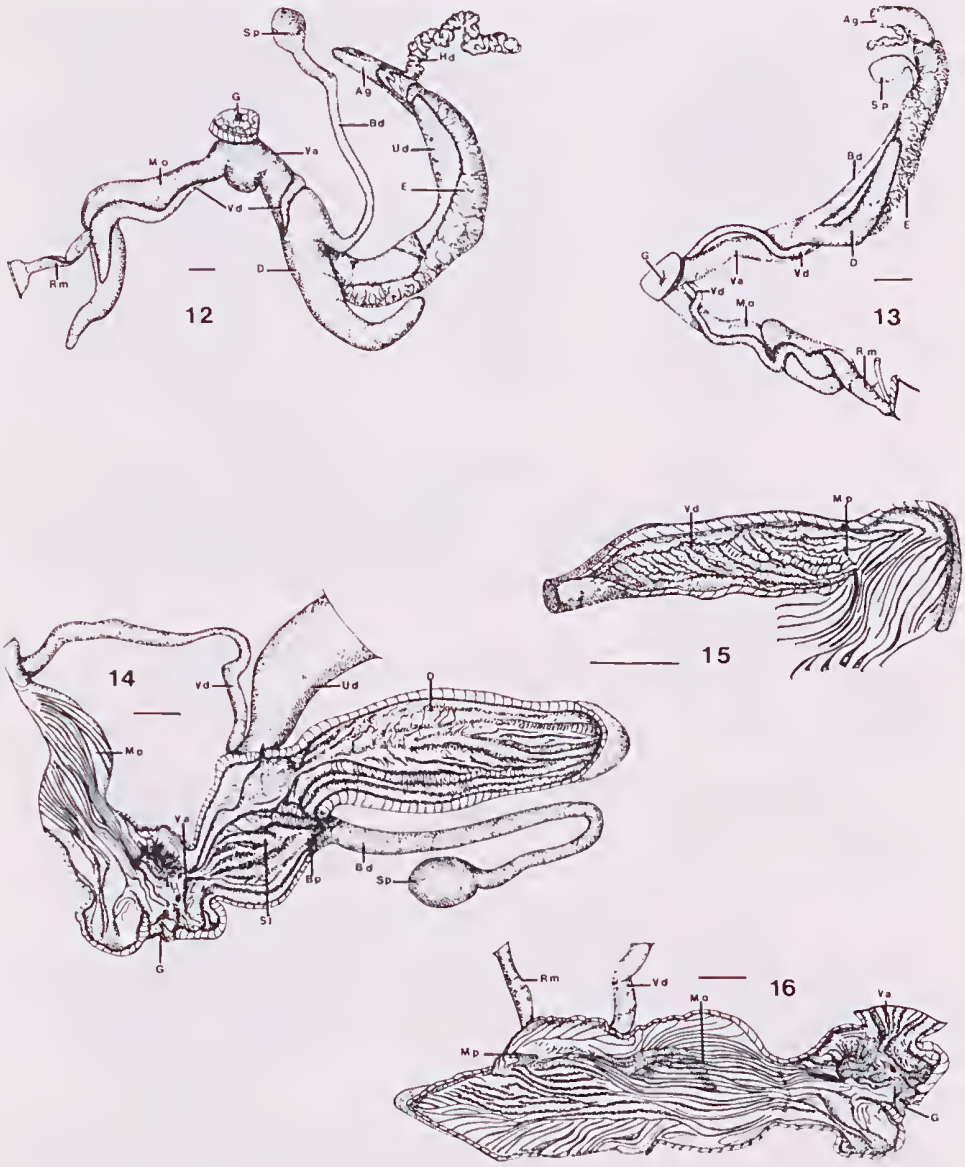


Figure 12. *Caryodes dufresnii:* genitalia, diverticulum (D) and bursa duct (Bd) separated from the common duct, scale 2 mm.
Figure 13. *Caryodes:* immature Florentine animal with small genitalia and a thin diverticulum. Note the reflexed penial apex. Scale line 2 mm.
Figure 14. *Caryodes dufresnii:* the vagina (Va), diverticulum (D) and busa duct pore (Bp): internal structure, scale 2 mm.
Figure 15. *Caryodes:* Mt. Field animal, epiphallic and male duct pore (Mp) structure, scale 2 mm.
Figure 16. *Caryodes dufresnii:* compound internal penial structure, scale 2 mm.

into the apex, the longitudinal pilasters are noticeably laterally impressed like miniature folds and a series of oblique unfolded pilasters is present. The bulging vas deferens ridge forms a false pilaster on which the penial pilasters are reduced and fade near the pore.

The Penial Retractor (fig. 12) is a relatively short stout rounded muscle attaching at about two-thirds the penial length 9 mm from the apical extremity. The point of attachment, near and between the point of vas deferens insertion and the male pore, is simple with no caecum. The muscle arises from the ventral lung diaphragm near the left flank.

Remarks: Pilsbury (1894) follows Semper's (1874) drawings of the anatomy. He does not recognise an epiphallus for *Caryodes* but does so in his description of *Hedleyella*. Pilsbury refers to an "adnate fleshy pillar, free at its distal end" which appears to describe the bulging wall of the vas deferens.

The male pore differs between various morphs as does the penial structure, the diverticulum length and structure and the vagina structure. There have been too few dissections to enable evaluation of these variations at present but some coincide with consistent shell differences requiring further study. However the subject of *Caryodes* shell variation is beyond the scope of this work.

THE CENTRAL NERVOUS SYSTEM

The circumoesophageal ring is not as elongate but more angled in disposition than is the case in *Anoglypta*. The commissures are soft thin and transparent not thickened into tough straps as in *Anoglypta*. The right parietal ganglion is noticeably the largest in most morphs being slightly larger than the visceral ganglion but the proportions seem more uniform throughout than in *Anoglypta*.

The cerebral ganglia have a thin dorsal surface flap which hides the bases of some nerves. The buccal ganglia were located on the ventral surface of the pedal ganglia with three commissures indentifiable on each side passing to the pleural, pedal and buccal ganglia from the cerebral. The differences between *Caryodes* and the apparent situation in *Anoglypta* are fundamental.

The dispostion of the nerves appears generally similar although some nerves are distinctly coiled. A nerve to the penis was traced from the right pedal ganglion and a nerve from the right cerebral ganglion may also insert on the penis but could not be confirmed in the material studied.

THE MUSCULAR SYSTEM

The buccal retractor rests in the centre of the foot and divides to each side of the buccal mass below the ganglionic mass. The flank retractors are very short and join the tentacle retractors within the foot then join the buccal retractor and finally the columellar muscle at the posterior extremity of the foot. There is a very short connector between the labial tentacle retractor and the right flank retractor in the gonopore region.

THE TYPE MATERIAL

The shell figured by Leach (1815) has a curious flattening of the basal margin which may be an artefact of the drawing as no similar undamaged specimen has been found. However this factor made selection of a suitable specimen for the neotype very difficult. Secondly it was necessary to ensure that the specimen could not have been collected by Peron. The matter was discussed (Kershaw, 1987) and considered unlikely but a copy of Ferussac's figures of the shells collected had not been seen at the time of publication. These shells prove to be of the small narrow based morph found near the coast on Maria Island. They bear little resemblance to the Leach drawing and could not be equivalent.

The consistent feature in the aperture of the neotype is the twisted columella. Although this feature does occur in other populations it would not have been possible for these to have been collected. It is not yet known if these morphs are closely similar in the anatomy.

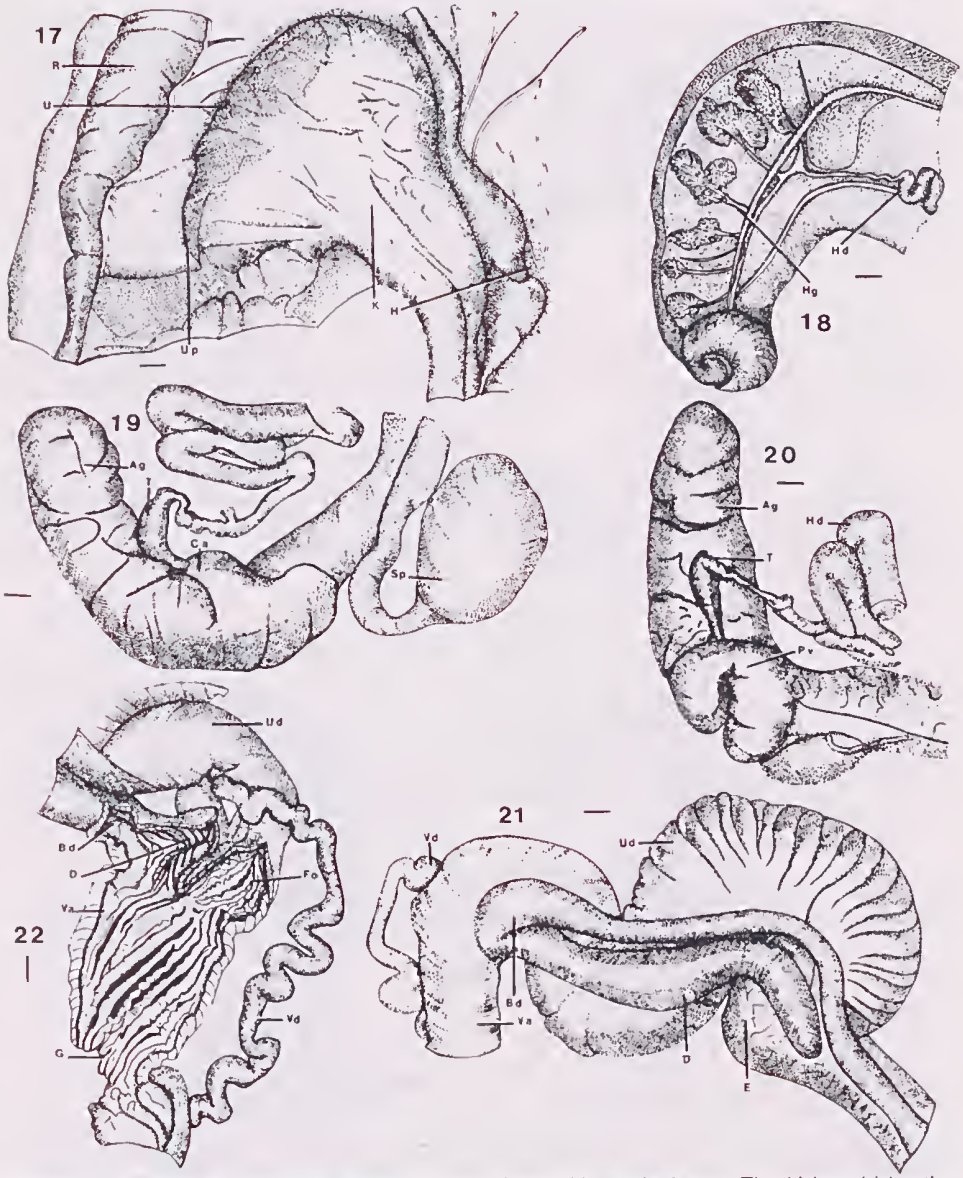


Figure 17. *Hedleyella maconelli:* kidney (K) and heart (H), scale 2 mm. The kidney hides the ureter (U).
Figure 18. *Hedleyella:* ovotestis (Hg) scale 2 mm.
Figure 19. *Hedleyella:* albumen gland (Ag), carrefour region (Ca) and bursa copulatrix (Sp), scale 2 mm.
Figure 20. *Hedleyella:* albumen gland (Ag), carrefour region and proximal common duct showing perivitelline gland (Pv), scale 2 mm.
Figure 21. *Hedleyella:* common duct with bursa duct (Sp) and diverticulum (D), scale 2 mm.
Figure 22. *Hedleyella:* internal structure of the vagina (Va) with the free oviduct (Fo), bursa duct (Bd) and diverticulum (D) pores, scale 2 mm.

Semper (1874) gave the Sandwich Islands as the type locality as noted by Hedley (1891). It is impossible to determine where Semper's specimen came from or to identity his otherwise useful drawings. Hedley (1891) figured the jaw and described a specimen of the small morph found near Hobart which is unlike the typical shell. Hedley (1892) added some comments on the bursa duct diverticulum but no further data were found which could assist in determining the nature of the typical species.

Genus *Hedleyella* Iredale 1914
Nomen novum for *Panda* Albers 1861, orthotype *Helix falconeri*
Gray 1834.

DIAGNOSIS

The shell is large globosely ovoid, umbilicate or imperforate, thin with the apex narrowly obtuse, the adult whorl and aperture very large. The protoconch sculpture of fine close spiral lirae cut into beads by fine radial striae continues into the adult becoming weaker as closer radial ridges develop.

Animal: A snail of the Caryodidae with elongate unicuspid teeth mounted on short broad basal plates with the marginal cusps and basal plates narrow and elongate. The penis has a conspicuous epiphallus closely attached longitudinally and inserted apically. The penial retractor inserts apically on the epiphallus not the penis. The male pore opens through a broadly lobed verge. The epiphallus is lined with several conspicuous pilasters. The bursa duct is more than twice the diverticulum length.

DISCUSSION

The shell of *Panda falconeri* was figured by Hedley (1892) and Pilsbry (1894). Pilsbry provided figures of the teeth and the genitalia. He describes the retractor as attached to the penis summit with the epiphallus inserting at the base of the retractor. The retractor in *Hedleyella maconelli* is attached to the epiphallus. Dartnall & Dartnall (1972) state only that the retractor and epiphallus are terminal. The radula of *H. maconelli* , very broad and the jaw large and orange coloured. Both Hedley (1892) and Pilsbry (1894) [illegible]t out that the penial retractor arises from the columellar retractor.

Hedleyella maconelli (Reeve 1853)
Dissected specimen collected by C. Horton about 16 kilometres east from Gympie, Queensland, about 610 mm below the surface of deep litter in dense rainforest, 7 November 1978.

THE SHELL

Diagnosis as for the genus.

DESCRIPTION

A 4.5 whorl globose pale brown shell marked with a pattern of interrupted dark bands. A full description is given by Cox (1868). The dimensions are:

Height 82.5 mm, maximum diameter 62.2 mm, minimum 48.7; aperture height 59 mm, width 36.4 mm.

Protoconch at least 2.5 worn whorls ending with an increase in density of radial lirae and whorl expansion. The first whorl is apparently almost smooth with developing wavy spiral lirae visible near the sutures by the second whorl crossed by very fine close radial striae. These become more clearly defined with raised radial lirae developing in the adult.

ANATOMY

The Pallial cavity is large elongate with a heavy collar, a well developed broad principal pulmonary vein and a dense pattern of brown coloured pulmonary venation. The kidney (fig. 17) is very broadly subtriangular with a rounded apex. The primary ureter empties into the

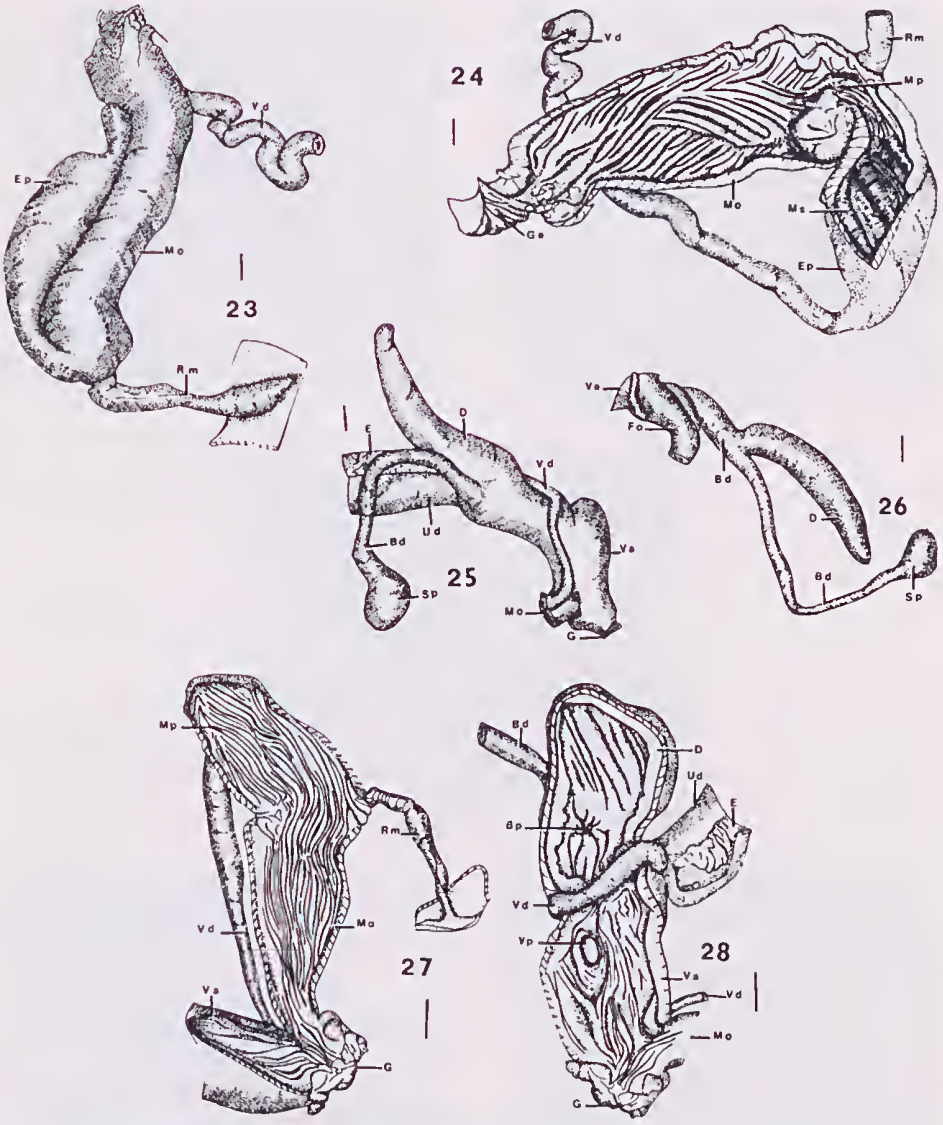


Figure 23. *Hedleyella:* penis (Mo), epiphallus (Ep) and retractor muscle (Rm), scale 2mm.
Figure 24. *Hedleyella:* internal structure of the epiphallus showing the pilasters (Ms), pore (Mp) and the penis (Mo), scale 2 mm.
Figure 25. *Caryodes:* Mt. Arthur animal, the bursa duct (Bd) — diverticulum (D) junction, scale 2 mm.
Figure 26. *Caryodes:* Forestier Peninsular animal, the bursa duct (Bd) — diverticulum (D) junction, scale 2 mm.
Figure 27. *Caryodes:* National Park animal showing simple longitudinal penial structure, scale line 2 mm.
Figure 28. *Caryodes:* National Park animal, diverticulum (D) — vagina (Va) internal structure, scale 2 mm. The vagina-bursa duct junction is very short.

pallial cavity through a defined pore close to the kidney base. There is no difference in configuration between *Hedleyella* and *Caryodes* but the latter is much more narrowly elongate. The *Hedleyella* heart valves extend two thirds the kidney length towards the apex. The dark brown digestive gland has a very dense texture.

REPRODUCTIVE ANATOMY

Apical Genitalia: The ovotestis (fig. 18) consists of 7 elongate lobes of pale brown loosely bunched elongate follicles embedded in the surface of the digestive gland. The cream hermaphrodite duct rests in very wide flattened coils against the orange coloured elongate (20 mm) digitiform albumen gland (fig. 19). The duct inserts with a cream coloured exposed inflated talon (2.5 by 2.2 mm) which then tapers over 2.5 mm on the surface to immerse and receives the albumen gland duct. The proximal gonoduct (fig. 20) junction has a bulging perivitelline gland resembling that of *Caryodes*.

THE SPERMOVIDUCT

The Common Duct (fig. 21) is elongate very sharply coiled with an inflated brownish cream mature uterus and cream prostate. It empties to an elongate (15 mm) free oviduct (15 mm) lined with about 10 tightly folded narrow pilasters which are sharpened at the pore (fig. 22).

The Bursa Copulatrix (fig. 19) is a large inflated brown ovoid body (14 mm by 12 mm) resting between the stomach and albumen gland.

The Bursa duct (figs. 18, 21) is a very long (59 mm) narrow duct attached to the common duct for most of its length to insert at a narrow pore between the pores of the free oviduct and the diverticulum. The bursa duct pore has one large and several very fine pilasters some of which enter the vagina (fig. 22).

The Bursa Duct Diverticulum (fig. 21) is narrowly elongate (27 mm) inflated to 4.7 mm diameter near its pore. The internal structure consists of a series of broad rounded fleshy pilasters which end abruptly at a transverse ridge near the pore. A broad pilaster passes laterally through the pore. This pilaster combines with a narrow bursa duct pilaster as it enters the vagina. Apart from this association the diverticulum appears as a distinct unit compressing the bursa duct against the free oviduct pore. In fact the bursa duct pore appears separated from the diverticulum by the expanded wall of the oviduct.

The Vagina (fig. 22) is short, broad (13 mm by 5.8 mm), somewhat cylindrical and 10% of the spermoviduct length. Internally it is lined with several rather broad longitudinal pilasters adjacent a series of narrower pilasters leading from the large free oviduct pore. Within the pore the pilasters are slightly folded. The vagina structure is continuous to the gonopore.

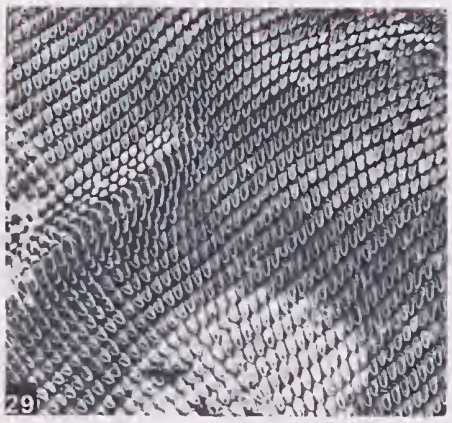
The Atrium (figs. 22, 24) although very shallow consists of the distinct very finely separated male and female openings set just within the gonopore entrance. The pilasters of both organs narrow to enter the region.

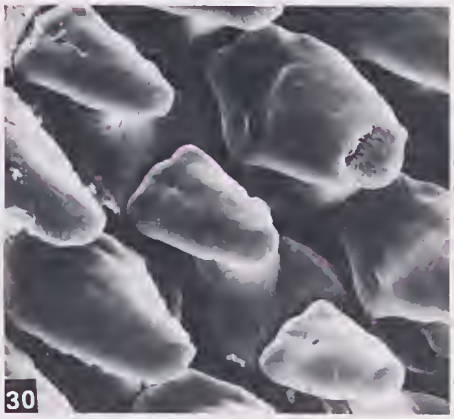
THE MALE GENITALIA

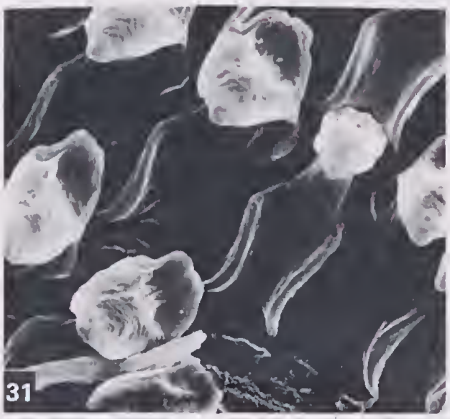
The Vas Deferens (figs. 22, 23, 24) is a very long (72 mm) duct immersed in the tissue after leaving the prostate, which curves abruptly from the oviduct near the free oviduct pore. It is strongly coiled on the vagina surface before passing below the penis to swell abruptly from 1.5 mm to the 4 mm diameter of the 21 mm long cylindrical epiphallus which curves along the penis to insert apically.

The Epiphallus (figs. 23, 24) is lined with about 10 fine rounded slightly spaced ridges which form large rounded pilasters consisting of very tightly packed narrow transverse folds. One of these is much wider and occupies a swollen section with thickened walls.

The Penis (figs. 23, 24) is about 25 mm long, somewhat cylindrical and swollen apically. Apically the lumen receives the male pore consisting of a large horn shaped papillate verge







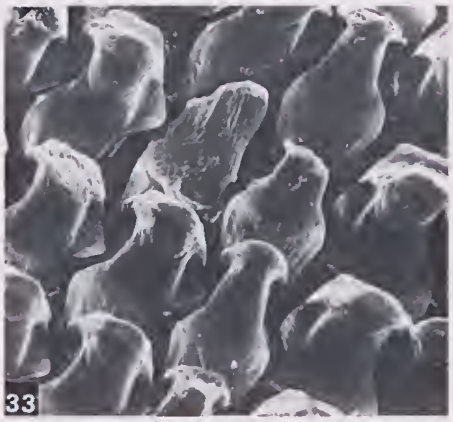
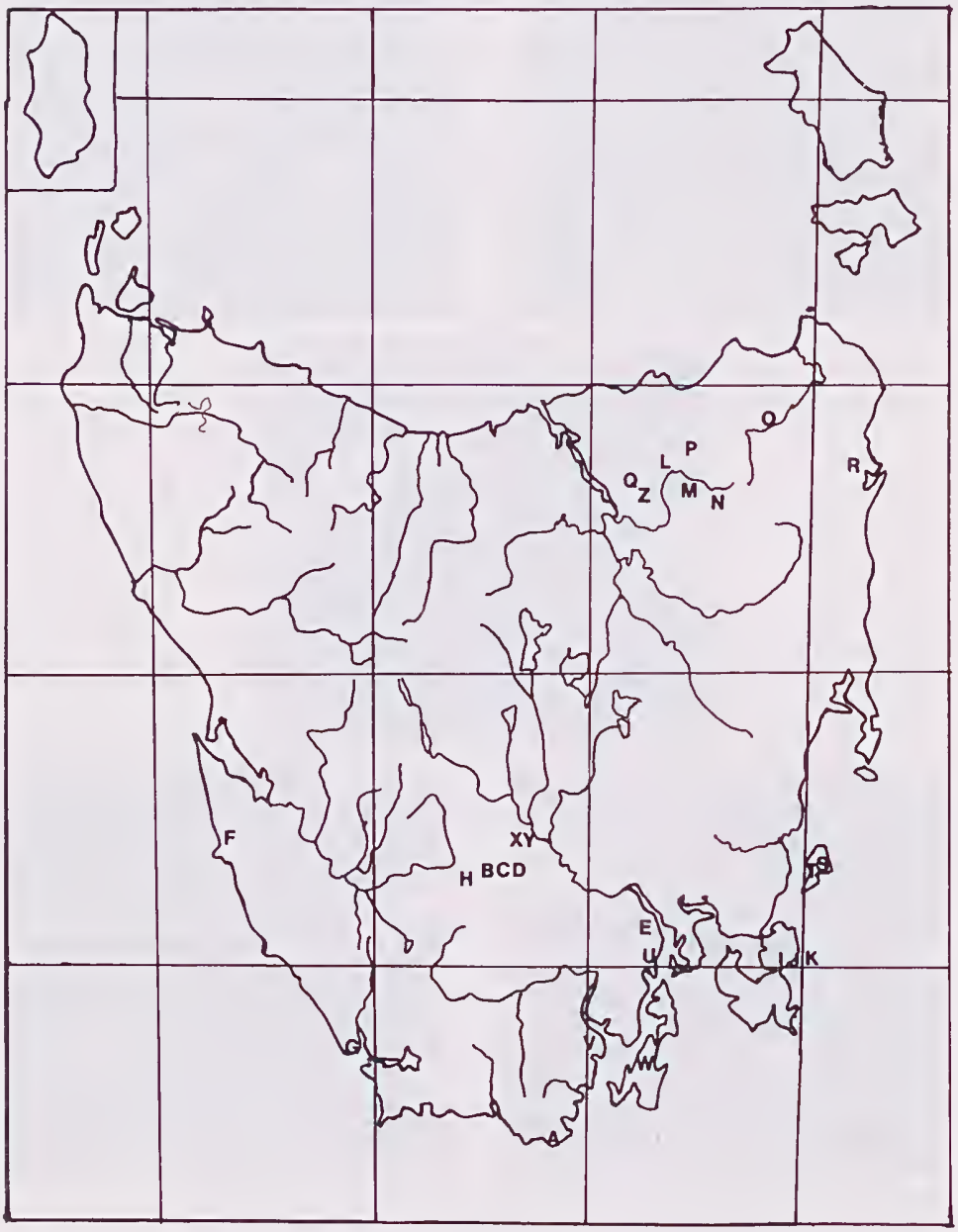


Figure 29. *Caryodes dufresnii:* radular teeth x 88. Photography A Daniell.
Figure 30. *Caryodes dufresnii:* central and first lateral teeth x 1100.
Figure 31. *Caryodes dufresnii:* teeth lifted showing the basal plates, x 880.
Figure 32. *Caryodes dufresnii:* marginal teeth x 1100.
Figure 33. *Caryodes dufresnii:* erosion and fracture of the radula teeth, x 880.


O
P
L
Q
Z
M
N
R
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XY
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BCD
E
U
K

cleft by a gutter from within the pore. The lumen is then lined with a complex of longitudinal and obliquely transverse flatly rounded pilasters which are longitudinally aligned basally.

The Penial Retractor (fig. 23) is a strong (15 mm) muscle arising on the pallial diaphragm wall to insert with a swollen muscular bulge on the epiphallus adjacent its insertion with the penis.

Remarks: In this animal the bursa duct diverticulum clearly opens at the vagina junction. The features of *Hedleyella* revealed by *H. maconelli* are as follows:

The ovotestis consists of 7 elongate lobes of elongate follicles. This seems to be consistent with the structure found in Caryodidae but differs from *Caryodes* in the elongate rather than globular appearance of the lobes.

The kidney is very broad.

The common duct is very sharply coiled.

The bursa duct is very long (compared with *Caryodes*) being of the order of 42% of the spermoviduct length.

The long narrow bursa duct diverticulum is almost 30% of the spermoviduct length.

A distinctly bulging epiphallus enters the elongate penis apically through a bulging verge. The epiphallic internal structure is distinct.

The penial retractor inserts apically on the epiphallus. The very short vagina is 9% of the spermoviduct length, only one third the equivalent proportion found in *Pygmipanda atomata* and half that found in *Caryodes dufresnii*.

COMPARATIVE ANALYSIS

1. Variation in the genus *Caryodes*.

Much has been made of shell variation but a proportion of this is superficial. There are two important factors to be considered. These include the shell size and the aperture.

There are two distinct levels of size which are related to the environment. Subsidiary to these there are variations in the fragility of the shell which may relate to other environmental factors such as calcium availability. The two levels of shell size have been used in the following discussion on anatomical variation.

Variation in the aperture is significant in that it affects the appearance of the shell. The presence or absence of noticeable twisting of the columella has been used by Iredale (1937) as a taxonomic feature. This will be discussed in the next part of this series. In general the aperture may be vertical or oblique and the columella may be twisted or not twisted. However there are a number of forms which have a slight columellar twist in some members of a population. This problem is not included here due to the complexity involved. In addition as the type form has been established on a high probability basis the matter need not be included in an essentially anatomical analysis.

In the lists of the 26 dissected animals (Table 1) and their dimensions (Table 2) both localities and specimens are identified alphabetically. A numerical list of comparative features used is given in Table 3 and a presence or absence comparative tabulation of these features in Table 4. The relationships, exclusive of taxonomic considerations, are summarised in the following group definitions. The neotype of *Caryodes dufresnii* is included in Group One.

Group One.

Snails with a large shell, the penis more than 50% of the vas deferens length having a complex internal structure, a few short distal pilasters enter the atrium, the transverse male pore not at the penial apex, the penial retractor insertion at less than 70% of the penial length from the atrium, usually complex vagina structure, the diverticulum medium to long with complex structure and the bursa duct long.

The specimens included are A: South Cape Bay; E: Mt. Wellington; F: East Hibbs Lagoon; G: Fowlers Point north of Port Davey. There is a reducing resemblance to specimen R; South Sister, specimen C: National Park and others.

Group Two.

Snails with a large shell, the penis greater than 70% vas deferens length having simple internal structure, a few long distal pilasters entering the atrium, the transverse male pore not at the penial apex, the penial retractor insertion at more than 70% of penial length from the atrium, complex vagina structure, the short diverticulum having simple structure and the bursa duct long.

Specimens B, C and D are all from forest near National Park. The penial structure (fig. 27) and the vagina-diverticulum structure (fig. 28) should be compared with these organs in A: South Cape Bay (figs. 14, 16).

Group Three.

Snails with a large shell, the penis more than 50% of vas deferens length having simple internal structure, a few long distal pilasters enter the atrium, the longitudinal male pore at or near the penial apex, the penial retractor insertion at more than 70% of penial length near the penial apex, the long diverticulum not near the bursa duct pore and the bursa duct long.

Specimens I, J, and K are all from the Forestier Peninsula north from Eaglehawk Neck. There is some resemblance to V: Esperance. The relationship between the diverticulum and bursa duct in these animals (fig. 26) is distinct compared to A: South Cape Bay (fig. 12) or L: Mt. Arthur (fig. 25).

Group Four.

Four a: Snails with a large shell, the penis between 50% and 70% of vas deferens length having an internal structure of longitudinal pilasters with fluted sides, a few short distal pilasters enter the atrium, the transverse male pore near the penial apex, the penial retractor insertion between 50% and 69% of penial length from the atrium, the long vagina with simple internal structure, the diverticulum structure simple and the bursa duct very long.

Specimen H: Timms Track, Florentine.

Four b: Snails with a large shell, the penis between 50% and 70% of vas deferens length having simple internal structure, a few short distal pilasters enter the atrium, the longitudinal male pore near or more than 20% penial length from the apex, the penial retractor insertion at more than 70% of the penial length from the atrium, the vagina structure simple or complex, the diverticulum structure simple or complex and the bursa duct short or long.

Specimens L: Mt. Arthur; M: Mt. Barrow; N: Ben Ridge; O: Winnaleah; the last two being juvenile may have unrecorded distinguishing features. Four a from the south west resemble Four b from the north east in the features of the penis excluding the retractor insertion site.

Group Five.

Five a: Snails with a large shell, the short penis less than 50% of vas deferens length having simple internal structure, a few long distal pilasters enter the atrium, the longitudinal male pore at the penial apex, the penial retractor insertion between 50% and 69% of the penial length from the atrium, the vagina structure simple or complex including a prominent pilaster, a short or long diverticulum with simple structure and a long bursa duct.

Specimens P: Sideling Range; Q: Underwood.

Five b: Snails with a small shell, the short penis less than 50% of vas deferens length having complex internal structure, a few long distal pilasters enter the atrium, the longitudinal male pore at the penial apex, the penial retractor insertion between 50% and 69% of the penial length from the atrium, the vagina structure long with simple internal structure including a prominent pilaster, a short diverticulum with simple structure and a very long bursa duct.

Specimen Z: Prossers Forest differs from Five a in the penial lumen structure. This animal will be dealt with in the next section of this work.

Group Six.

Six a: Snails with a large shell, the penis less than 50% of the vas deferens length having simple internal structure, a few short distal pilasters enter the atrium, the longitudinal male pore

near the penial apex, the penial retractor insertion more than 70% of the penial length from the atrium, the short vagina with simple structure including a prominent pilaster, the long diverticulum with simple structure and a long bursa duct.

Specimen T: Mt. Maria.

Six b: Snails with a small shell, the penis less than 50% of the vas deferens length having simple internal structure, a few long distal pilasters enter the atrium, the longitudinal male pore at or near the penial apex, the penial retractor insertion between 50% and 90% of the penial length from the atrium, the long vagina with simple structure including a prominent pilaster, the diverticulum structure simple and long bursa duct.

Specimens S: near Darlington, Maria Island; X, Y: Ellendale. The Ellendale specimens differ in the male pore but resemble V: Esperance in this feature.

Group Seven.

Seven a: Snails with a small shell, the penis between 50% and 70% of the vas deferens length having a complex internal structure, the transverse male pore near or not near the penial apex, the penial retractor insertion between 50% and 90% of the penial length from the atrium, the long vagina with simple structure with or without a prominent pilaster, the diverticulum structure simple and a long bursa duct.

Specimens U: Bonnet Point near Kingston; V: Esperance.

Seven b: Snails with a large shell, the penis between 50% and 70% of the vas deferens length having a complex internal structure, the transverse male pore more than 20% of the penial length from the apex, the penial retractor insertion between 50% and 69% of the penial length from the atrium, the long vagina with simple structure including a prominent pilaster, the diverticulum structure simple and a long bursa duct.

Specimen W: Bruny Island. The major difference between individuals of Group Seven and between Group Seven and Group One rests in the male pore location and the shell size. In general terms W: the Bruny Island specimen most resembles V: the Esperance specimen excluding size.

In grouping the specimens most weight has been given to the penial features. Secondly the features used appear to reflect possible species recognition features most. However it must be emphasized that although some of these animals exhibit marked differences, they cannot be evaluated without a series of dissections from each population. Several dissections from some populations have been completed but the variation seen is insignificant for the penial features listed. The internal penial morphology illustrated in Figure 27 is distinct compared to typical *Caryodes dufresnii* as illustrated in Figure 16.

A comparison with the penis of genus *Acavus* Randles 1900 suggests a more complex penis in *Caryodes* but both have a range of different forms. Various of these forms have a fluting or corrugation of the pilasters reminiscent of that illustrated for species of *Acavus*.

The kidney and ureter of *Acavus* (Randles 1900) do not appear directly comparable with these organs of *Caryodes*.

Generic Comparisons.

A number of genera have been introduced within the family Caryodidae but the validity of some has been questioned (Dartnall & Dartnall 1972). The stable genus *Anoglypta* has been compared with the discoid shelled *Pedinogyra* from New South Wales (Kershaw 1988). *Caryodes* is compared herein with the more or less bulimuliform *Hedleyella* from New South Wales and Queensland. A similar study of Victorian *Pygmipanda* is in preparation. Projected studies of the pyriform *Brazieresta* and the reduced *Pandofella* are proposed as these become available. There is a noticeable general resemblance between all these genera which questions the degree of relationship.

Solem (1969) included *Pygmipanda, Brazieresta* and *Pandofella* within *Hedleyella* in a synopsis of the Acavidae. Later (Solem 1978) he separated the Acavidae and Caryodidae. Smith

(1971) suggested that *Brazieresta* may belong with *Pygmipanda*. The clear relationship between *Pedinogyra*, *Pygmipanda* and *Hedleyella* is evident. *Pedinogyra* has a suggestion of bulimuliform morphology but has evolved to a planate form while retaining an umbilicus and losing the strong sculpture of *Anoglypta*.

Caryodes has retained the ancestral sculpture to a significant degree and may have developed a bulimuliform or pyriform morphology independently. Of the two accepted species of *Hedleyella* the broadly globose sub-auriform *H. falconeri* has retained the umbilicus while the globose bulimuliform *H. maconelli* has lost this feature. These morphs suggest transitional experiments between a discoid umbilicate and an imperforate pyriform morphology. The pyriform imperforate *Brazieresta larreyi* may represent a further stage. Finally the few whorled *Pandofella whitei* has also lost the umbilicus and is in the process of losing the shell. Between these extremes there are the series of shapes discussed by Hedley (1892).

The Umbilicus in Shells of *Caryodes*.

Most morphs of *Caryodes* are imperforate in the adult. However a clear umbilical chink occurs in the Ben Lomond shell and in an extinct morph from Conara. This suggest a much wider past distribution for this morph. Some very juvenile shells of *Caryodes* possess an umbilicus and a primitive conical appearance suggestive of the relationship with *Anoglypta*. The columellar reflection in *Caryodes* varies from a thin glaze to a thickened raised callus. The juvenile umbilicus is covered by the reflection with growth. The Ben Lomond shell has a thickened reflection which has developed in such a way as to retain the umbilical chink.

There appear to be several groups within the Caryodidae, each having a characteristic shell and colour pattern and retaining ancestral features in parallel with the others. The apex in all the shells studied reveals a degree of similarity. The two Tasmanian forms retain a conspicuous banding pattern while the mainland forms have a possible derivative of this. The validity of such an hypothesis will require considerable investigation.

The Caryodidae Animal.

The preliminary investigation undertaken in this work suggests that the carrefour region and proximal oviduct found in *Anoglypta* is much simpler than that of *Caryodes*. In this respect *Caryodes* appears similar in development to *Hedleyella* and *Pygmipanda*. The *Caryodes* carrefour enters a bulging region which is similar to that described by Tompa (1984) as "the perivitelline membrane gland". . ."often S-shaped" at the "posterior". The appearance in *Caryodes* (fig. 11) is less like the figure of *Anguispira* (Tompa 1984, fig. 11; Solem 1976) than is that of *Hedleyella* (fig. 19). This region may be important in dealing with generic status but requires detailed investigation.

Also requiring detailed investigation the bursa duct diverticulum, regarded as an important family feature in the Caryodidae, has degrees of distinction between the genera. Compared with *Caryodes*, *Anoglypta* has this gland small, reversed and its internal structure ends abruptly at its pore. This is not necessarily the case with *Caryodes* and the structure may continue into the bursa duct or even into the vagina junction region. Davies (1914) described a transverse section of the gland of a *Caryodes* animal from Esperance, southern Tasmania but no further study is known.

The observations made in the current work have shown that the diverticulum varies in its relationship to the bursa duct pore, the complexity of its internal appearance, the length, shape and degree of coiling as well as the relationship of its structure to the bursa duct. At least in terms of relationship to the bursa duct pore there is some evidence of distinction between the genera. However an observation based on only one Hedleyella dissection is inadequate. Secondly the differences listed suggest a population recognition feature if consistent with penial differences. This concept is supported by the dissections so far completed on Forestier Peninsula *Caryodes*.

The *Caryodes* vagina has revealed a series of distinctions between populations in such features as complexity of the internal structure, the presence or absence of a short bold pilaster, its position and the presence of a pocket in the wall. Some of these features appear confined

to *Caryodes*. The structure of that section of the vagina related to the free oviduct pore is distinguishable from the balance. The manner of this relationship appears distinguishable between *Caryodes* and *Hedleyella*.

The epiphallic and male pore region of the vas deferens is the most significant on a taxonomic basis. This area has noticeable points of distinction between *Caryodes, Hedleyella* and *Pygmipanda*. In addition various populations of *Caryodes* reveal points of difference at the pore. The structure of the pore differs between *Caryodes* and *Anoglypta*. There is a difference in the apparent orientation of the pore between *Caryodes* populations from north and east Tasmania compared to the south and south west.

Finally Connolly (1915) noted the resemblance between the jaw of *Pedinogyra* and that of *Anoglypta*, the extent to which the vas deferens is embeddd in the penial wall of *Anoglypta* and that the penial retractor arises from the columellar muscle or far back on the lung floor, among other comparisons with the Acavidae. He also observed that ectocones can be distinguished in the marginal teeth of some specimens of *Anoglypta* but this has not been noticed in the current study.

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TABLE 1.

Caryodes: Dissected Specimens: List of Localities.

Specimen	Locality	Tasmap Sheet	Grid	Forest type
A	South Cape Bay	South Cape	83000.73000	wet
B	National Park	Tyenna	76800.74700	mixed
C	National Park			
D	National Park			
E	Mt. Wellington	Derwent	21000.48000	wet
F	E. Hibbs Lagoon	Spero	62100.85700	rain
G	Fowlers Point	Port Davey	12700.07900	wet
H	Florentine	Wedge	51400.70700	wet
I	Forestier Pen	Storm Bay	75800.38400	wet
J	Forestier Pen			
K	Forestier Pen			
L	Mt. Arthur	Pipers	20500.31800	wet
M	Mt. Barrow	Pipers	35700.20100	rain
N	Ben Ridge	Forester	47600.23500	rain
O	Winnaleah	Forester	76400.44300	rain
P	Sideling Range	Pipers	35200.31200	wet
Q	Underwood	Pipers	17000.28500	wet
R	South Sister	Break O' Day	98500.00200	wet
S	Maria Island	Maria	91000.88000	dry
T	Mt. Maria	Maria	91000.28000	scree
U	Kingston	Derwent	27450.41800	woodland
V	Esperance	D Entrecasteaux	02300.00800	dry
W	Bruny Island	D Entrecasteaux	26000.99000	wet
X	Ellendale	Tyenna	74900.84600	dry
Y	Ellendale			
Z	Prossers Forest	Pipers	16400.24100	dry

(n.b. The forest types are rainforest, mixed forest, wet sclerophyll, dry sclerophyll and sclerophyll woodland.)

TABLE 2.

List of Shell Dimensions and Collectors.

	SHELL		Aperture		Collector	Date
	Whorls	Ht	Diam	Ht	Diam	
A	5.25	36.0	19.1	19.0	9.4	J. Burrell 30-vi-1973
B	5.12	35.4	23.8	19.6	13.6	R. C. Kershaw 7-xi-1975
C	5.00	34.0	19.7			R. C. Kershaw 7-xi-1975
D	5.00	35.0	21.4	19.1	11.4	R. C. Kershaw 7-xi-1975
E	5.25	38.3	22.7	20.0	14.1	K. Bonham 21-iv-1987
F	5.25	42.0	24.5	21.7	14.1	S. Smith 8-i-1987
G	5.25	34.3	19.5	17.7	11.9	S. Smith 13-ii-1987
H	5.25	32.9	17.4	16.5	9.5	S. Hunniford & C. Leaman 15-xi-1986
I	5.25	34.5	19.9	17.0	10.0	R. C. Kershaw 26-iv-1975
J	5.50	41.0	22.4	18.0	10.2	R. C. Kershaw 26-iv-1975
K	5.37	40.0	23.2	21.5	12.4	R. C. Kershaw 26-iv-1975
L	5.37	43.5,	25.5	21.0	14.4	R. C. Kershaw 18-xi-1984
M	5.25	19.7	19.0	16.5	10.0	R. C. Kershaw 18-iv-1980
N	4.87	24.4	16.5	16.0	7.2	R. C. Kershaw 3-xi-1984
O	4.50	21.4	16.9	14.2	8.8	E. Armstrong R. Farquahar 10-xi-1976
P	4.87	35.0	21.9	18.8	11.0	R. C. Kershaw -iii-1976
Q	5.50	38.0	21.5	19.9	10.7	I. Norton -xi-1980
R	5.25	43.3	25.4	22.4	12.5	R. C. Kershaw A. J. Dartnall 20-v-1984
S	5.00	24.3	14.1	13.2	8.0	C. Spry 15-vi-1986
T	5.00	37.4	22.3	21.0	12.1	C. Spry 21-iv-1986
U	5.00	22.3	13.8	12.1	7.3	K. Bonham 10-v-1987
V	4.75	27.4	17.1	14.3	9.2	K. Bonham 10-v-1987
W	5.00	33.1	19.1	18.5	12.6	J. Campbell 13-iv-1985
X	4.90	24.0	13.8	12.0	8.0	R. C. Kershaw 1-xi-1975
Y	5.00	26.0	15.0	14.0	8.0	R. C. Kershaw 1-xi-1975
Z	5.00	24.6	15.5	13.5	9.1	R. C. Kershaw 27-ix-1986

TABLE 3.

Key to Comparative features used in Group Definitions.

Kidney narrowly elongate . . . 1
elongate triangular . . . 2
broad . . . 3
Pericardium two/thirds kidney . . . 4
three/quarters kidney . . . 5
four/fifths kidney . . . 6
Penis long . . . 7
medium . . . 8
short . . . 9
Penis internal structure simple longitudinal pilasters . . . 10
Longitudinal pilasters with fluted sides . . . 11
compound oblique and longitudinal + or − fluting . . . 12
Penis few short distal pilasters enter atrium . . . 13
few long distal pilasters enter atrium . . . 14
Male Pore at penial apex—11% or less of penial length . . . 15
near apex — at 12% to 20% of penial length . . . 16
at < 20% of penial length from apex . . . 17
transverse in orientation . . . 18
longitudinal in orientation . . . 19
Penis < 50% vas deferens length . . . 20
50% to 70% vas deferens length . . . 21
> 70% vas deferens length . . . 22
Penial Retractor at < 50% penial length from atrium . . . 23
at between 50% and 69% penial length . . . 24
at > 70% of penial length from atrium . . . 25
near or adjacent the apex . . . 26
Vagina internal structure simple . . . 27
complex . . . 28
includes a prominent pilaster . . . 29
includes a pocket in the wall . . . 30
Vagina short, < 20% spermoviduct length . . . 31
long, > 20% spermoviduct length . . . 32
Free Oviduct short, 3 mm or less . . . 33
long, > 3 mm . . . 34
Diverticulum short, 26% or less spermoviduct length . . . 35
medium, between 26% and 50% spermoviduct . . . 36
long, > 50% spermoviduct length . . . 37
internal structure simple longitudinal . . . 38
internal structure complex . . . 39
situate at or near bursa duct pore . . . 40
not at or near bursa duct pore . . . 41
Bursa Duct short, 50% or less spermoviduct length . . . 42
long, between 50% and 69% spermoviduct length . . . 43
very long, 70% or more of spermoviduct . . . 44
Shell large at 5 or more whorls, > 30 mm length . . . 45
small at 5 or more whorls. < 30 mm length . . . 46
Habitat rainforest . . . 47
wet sclerophyll forest . . . 48
dry sclerophyll forest . . . 49
coastal scrub or woodland . . . 50

TABLE 4.

Presence or Absence Tabulation of Anatomical Features.

Sp: Item	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
1		/	/	/	/	/						/	/	/	/							/				/
2	/																				/		/	/	/	
3									/	/	/															
4		/	/	/	/	/																				
5									/	/	/		/	/	/									/	/	/
6	/																				/	/	/			
7	/	/	/	/	/		/			/	/															
8						/		/	/			/	/					/	/	/	/	/	/	/	/	
9																/	/									/
10		/	/	/					/	/	/	/	/			/	/		/	/				/	/	
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List of Abbreviations

Ag — albumen gland
Ao — aorta
Au — auricle
Bd — bursa duct
Bp — bursa duct pore
Ca — carrefour region
Cm— columellar muscle
D — diverticulum
E — prostate
Ep — epiphallus
Fo — free oviduct
G — gonopore
Ga — genital atrium
H — pericardium
Hd — hermaphrodite duct
Hg — ovotestis
I — intestine
K — kidney
L — lung region
Lv — main pulmonary vein
Md— male duct
Mo— penis
Mp— male duct pore
Ms — epiphallic pilasters
O — oesophagus
Ot — occular tentacle
Or — occular tentacle muscle
Pv — perivitelline gland
R — rectum
Rm— penial retractor muscle
S — stomach
Sa — salivary gland
Sj — Bursa-vagina junction
Sp — bursa copulatrix
T — talon
U — primary ureter
Ud — oviduct (uterus)
Up — ureter pore
Va — vagina
Vd — vas deferens
Ve — ventricle
Vp — vagina pilaster